

NOTES ON THE BREEDING SYSTEMS OF *SACOILA LANCEOLATA* (AUBLET) GARAY (ORCHIDACEAE)¹

PAUL M. CATLING²

ABSTRACT

To document breeding systems in the widespread neotropical terrestrial orchid, *Sacoila lanceolata*, pollination and seed development were studied in the field and in cultivated plants. In the southern Florida study area, plants of var. *lanceolata* were not pollinated and hummingbird pollinators were apparently absent. When plants from southern Florida were moved to a situation where hummingbirds were abundant in southern Ontario, hummingbird-pollination was observed on numerous occasions and the incidence of pollination was approximately 90%. Pollination experiments demonstrated a reliance on pollen vectors in plants of var. *lanceolata* from central Guyana, where a variety of hummingbird pollinators are available, but the plants of the same variety from southern Florida were found to be agamospermic. Examination of serial sections of ovaries in successive developmental stages indicated that agamospermy is by adventitious embryony, the embryos (one or more) being formed by proliferation of the inner integument. Adventitious embryony can be detected through association with polyembryonic seed, is characteristic of Florida populations of var. *lanceolata*, and occurs also in portions of the tropical range. Plants of *S. lanceolata* var. *paludicola* from southern Florida were found to self-pollinate. The pollinator-independent breeding systems in southern Florida populations of *S. lanceolata* var. *lanceolata* and var. *paludicola* and the apparent absence of races totally reliant upon pollen vectors are associated with pollinator-paucity.

Sacoila lanceolata (Aublet) Garay var. *lanceolata* is a reddish- to orange-yellow- or occasionally pale greenish-flowered, terrestrial orchid with a broad neotropical distribution extending from northern Florida and northern Mexico to northern Uruguay (Luer, 1972). The smaller-flowered var. *paludicola* Luer is restricted to extreme southern Florida [the Fakahatchee Strand in Collier Co. (Luer, 1971a), Kendall Hammock in Dade Co. (pers. obs.), and from one location in the Everglades (McCartney, 1985)] and the Caribbean region (based on examination of specimens at AMES, DAO, SEL, and FTG—acronyms from Holmgren et al., 1981). Both var. *lanceolata* and var. *paludicola* have gaping tubular flowers with an adnate spur (Fig. 1). In terms of flower color and morphology and absence of a detectable odor, the flowers of both varieties are representative of the bird pollination syndrome (Pijl & Dodson, 1966).

Casual observations of seed development in a few cultivated plants that were maintained in the absence of any potential pollen vectors suggested that both var. *lanceolata* and var. *paludicola* may

have pollinator-independent breeding systems in southern Florida. Since the breeding systems of tropical and subtropical terrestrial orchids are relatively poorly known, a study was undertaken to document the breeding systems of *S. lanceolata*.

METHODS

FIELD STUDIES OF POLLINATION IN SOUTHERN FLORIDA

In order to gather information on natural pollination, populations of *S. lanceolata* var. *lanceolata* were observed for an overall total of 20 hours in southern Florida during mid-May 1978 and 1984. The presence of potential pollinators, including hummingbirds and large bees particularly, was noted. Large bees are the regular pollinators of some related species (Pijl & Dodson, 1966; Catling, 1983).

Since pollination of orchid flowers involves removal of the pollinarium from the anther, it is possible to obtain an approximation of the incidence of pollination by recording pollinaria

¹ Living plants of *Sacoila lanceolata* var. *paludicola* were provided by C. A. Luer, H. Brown, and G. Matous. C. A. Luer and V. R. Brownell assisted with field work. Useful criticisms were provided by S. C. H. Barrett (University of Toronto), C. A. Luer (Missouri Botanical Garden), N. R. Morin (Missouri Botanical Garden), and N. H. Williams (Univ. of Florida). W. Wojtas kindly assisted with the anatomical work.

² Agriculture Canada, Biosystematics Research Institute, Central Experimental Farm, Ottawa, Ontario, Canada K1A 0C6.



FIGURE 1. A, B, D. *S. lanceolata* var. *lanceolata*.—A. Frontal view of flowers, Immokalee, Collier Co., Florida, 15 May.—B. Flower spike of cultivated plant from central Guyana, South America, 13 January.—D. Side view of flowers, Immokalee, Collier Co., Florida, 15 May.—C. *S. lanceolata* var. *paludicola*, flower spike, cultivated plant from Fahkahatchee Strand, Collier Co., Florida, 15 February.

removal. This is more easily recorded than the presence of pollen tubes in the deteriorating column of faded flowers. It is, however, only an approximation since pollinaria removal is occasionally (although apparently rarely) prevent-

ed by malformation or drying out of the viscidium or by the difficulty of attaching to an existing excess load of pollinaria. The incidence of pollination in southern Florida, as determined by the absence of the pollinaria in faded flowers,

was determined by examining 500 flowers from a total of 100 inflorescences representing eight locations.

STUDIES OF POLLINATION OF TRANSPLANTS

Plants from the Sarasota and Immokalee areas of southern Florida were observed for approximately 33 hours after transplanting into a rural setting in southeastern Ontario, Canada, in late May 1984. The presence of potential pollinators was again recorded. The approximate incidence of pollination was determined by pollinaria removal (see above) in five groups of five experimental plants each, including a total of 429 flowers.

POLLINATION EXPERIMENTS

Pollination experiments were performed on plants maintained in a glass house in Ottawa in April and May 1984 from which potential pollinators (insects, hummingbirds) were excluded. Voucher specimens are contained in the Agriculture Canada herbarium of the Biosystematics Research Institute in Ottawa, Ontario (DAO). The experiments were performed on three groups of plants: 1) 60 plants of *S. lanceolata* var. *lanceolata*, four from each of 15 localities in southern Florida distributed in a broad band, ca. 30 km wide, from Sarasota south to Immokalee; 2) three plants of *S. lanceolata* var. *lanceolata* from near Mahdia, central Guyana, South America; and 3) six plants of *S. lanceolata* var. *paludicola* including three from the Fahkahatchee Strand, Collier Co. and three from Kendall Hammock, Dade Co., both in southern Florida.

Starting from the base of a spike, each sequence of five flowers was treated in the same way. Following the first day after all flowers in the sequence had fully opened, the first flower was left undisturbed, the pollinarium was removed from the second flower, the third was self-pollinated, the fourth pollinated with pollen from a different flower on the same plant (geitonogamous pollination), and the fifth was pollinated with pollen from a flower on a different plant (cross-pollination). With the exception of the plants from Guyana, cross-pollination was carried out using plants from different localities. Each ovary was appropriately tagged to indicate the treatment of the corresponding flower. The number of expanded ovaries was recorded as well as the percentage of embryo sacs containing embryos. The latter value was estimated by emp-

tying the capsule and determining the presence or absence of embryos in the first 200 embryo sacs observed. This was followed by a scan of a few thousand to make certain that the value obtained was representative. If the value was considered not representative, two more samples of 200 were scored and the average percentage was then recorded.

ANATOMICAL STUDY

Each of the three groups of plants used in the pollination experiments was studied anatomically to determine whether or not pseudogamy (asexual seed development requiring pollination) was operating and to determine the method of agamospermy in plants producing seed without any pollination. Serial sections of ovaries were examined in successive developmental stages. Ovaries fixed and preserved in formalin-acetic acid-alcohol (FAA) were dehydrated, embedded in paraffin, sectioned, mounted, and stained using a safranin-hematoxylin combination (Lillie, 1969; Jensen, 1958). Mature seeds of experimental plants were stained for examination using the differential stain technique described by Owczarzak (1952). The percentage of polyembryonic seed was determined in the same way as the percentage of embryo sacs containing embryos (see above).

STUDY OF DRIED MATERIAL

An attempt was made to determine the distribution of breeding systems through the examination of herbarium material from AMES, MICH, SEL, FTG, and DAO (acronyms from Holmgren et al., 1981). This is made possible, to a degree, by association of various morphological features with a specific breeding system. Plants were considered agamospermic if they possessed any polyembryonic seed. Relatively small flower size was considered potentially indicative of autogamy (see Ornduff, 1969). Lack of expansion of some ovaries in fruiting material was considered suggestive of obligately cross-pollinated races.

RESULTS

FIELD STUDIES OF POLLINATION IN SOUTHERN FLORIDA

In southern Florida, insects (including larger bees) were present but were not observed visiting the flowers of *S. lanceolata* var. *lanceolata*. No

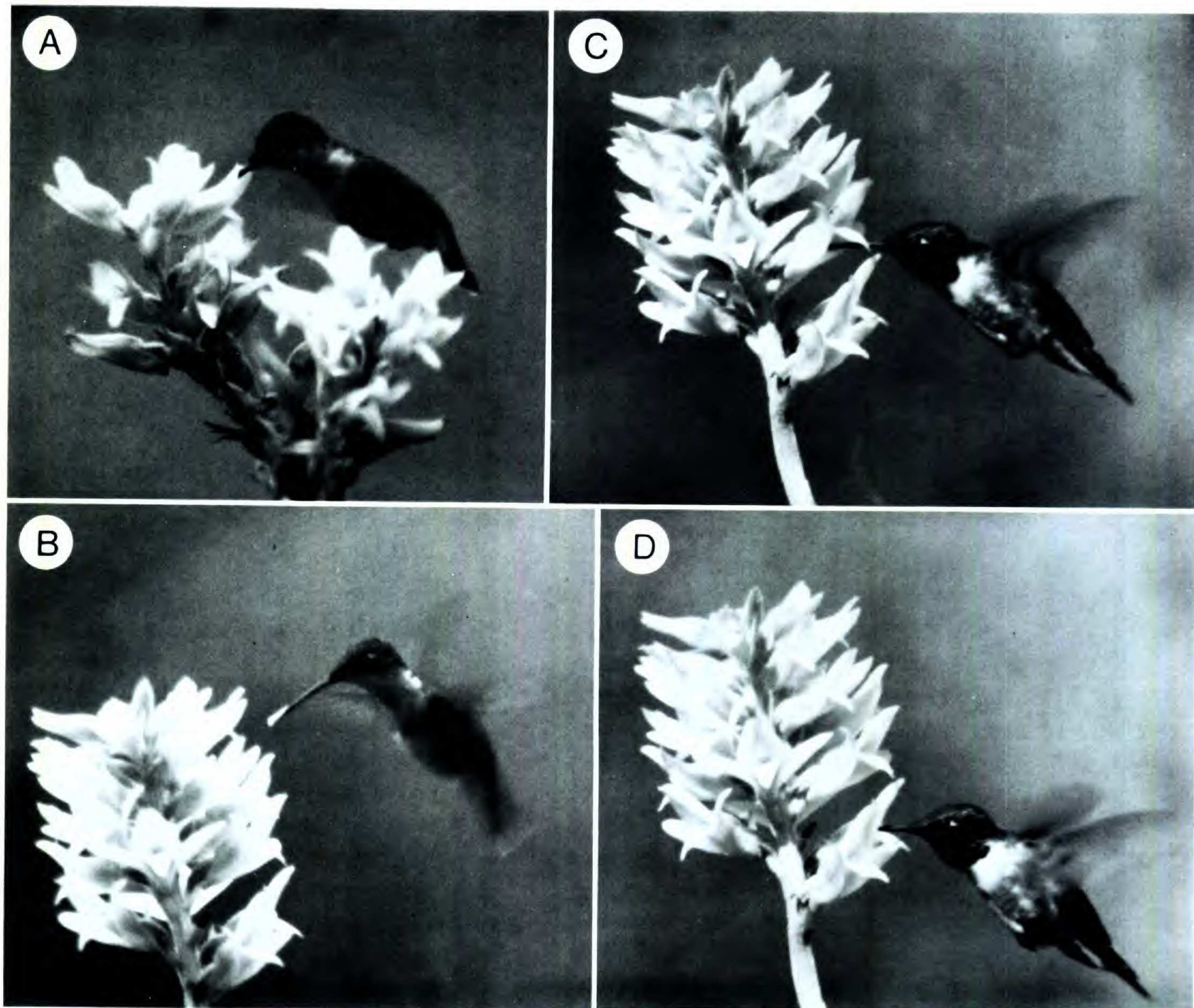


FIGURE 2. Ruby-throated Hummingbird (*Archilochus colubris*) pollinating *Sacoila lanceolata* var. *lanceolata* from Sarasota Co., Florida, 25 May.—A. Female probing flower directly through the floral tube.—B. Female withdrawing with a pale yellowish pollinia attached to the tip of the bill.—C. Male probing a flower from the right side below the lip.—D. Male probing flower directly.

hummingbirds were observed. There was no evidence of pollination, in the form of pollinarium removal, in any of the eight southern Florida locations.

STUDIES OF POLLINATION OF TRANSPLANTS

In southeastern Ontario, large insects including large bees were common, but they totally ignored the flowers. Ruby-throated Hummingbirds (*Archilochus colubris*) were also common. These birds regularly visited the flowers of *S. lanceolata* var. *lanceolata* and acted as effective pollinators. Females were observed visiting inflorescences on 25 separate occasions and males on 46. A visit usually involved probing three to five flowers on an inflorescence and visiting one to three inflorescences in a group of five. Visits

were 15 minutes to two hours apart and were most regular in the morning between 9 A.M. and 11:30 A.M. Visits by one or more females (i.e., female visits) involved a direct probing of the flowers (Figs. 2A, 3A), the pollinia becoming attached, by the elongate cushion-type viscidium that sheaths the rostellum (Fig. 3C, D, E, and Greenwood, 1982), to the distal portion of the bill (Figs. 2B, 3B). Male visits involved probing from the side and below the lip approximately 50% of the time (Fig. 2C, D). Probably as a consequence of this "robbing," male visits resulted in pollinia removal only eight of 46 times, as compared with 15 of 25 in the case of female visits. In the 25 experimental plants, which were observed being pollinated by the hummingbirds, the incidence of pollination was 90% (i.e., 386 of 429 flowers).

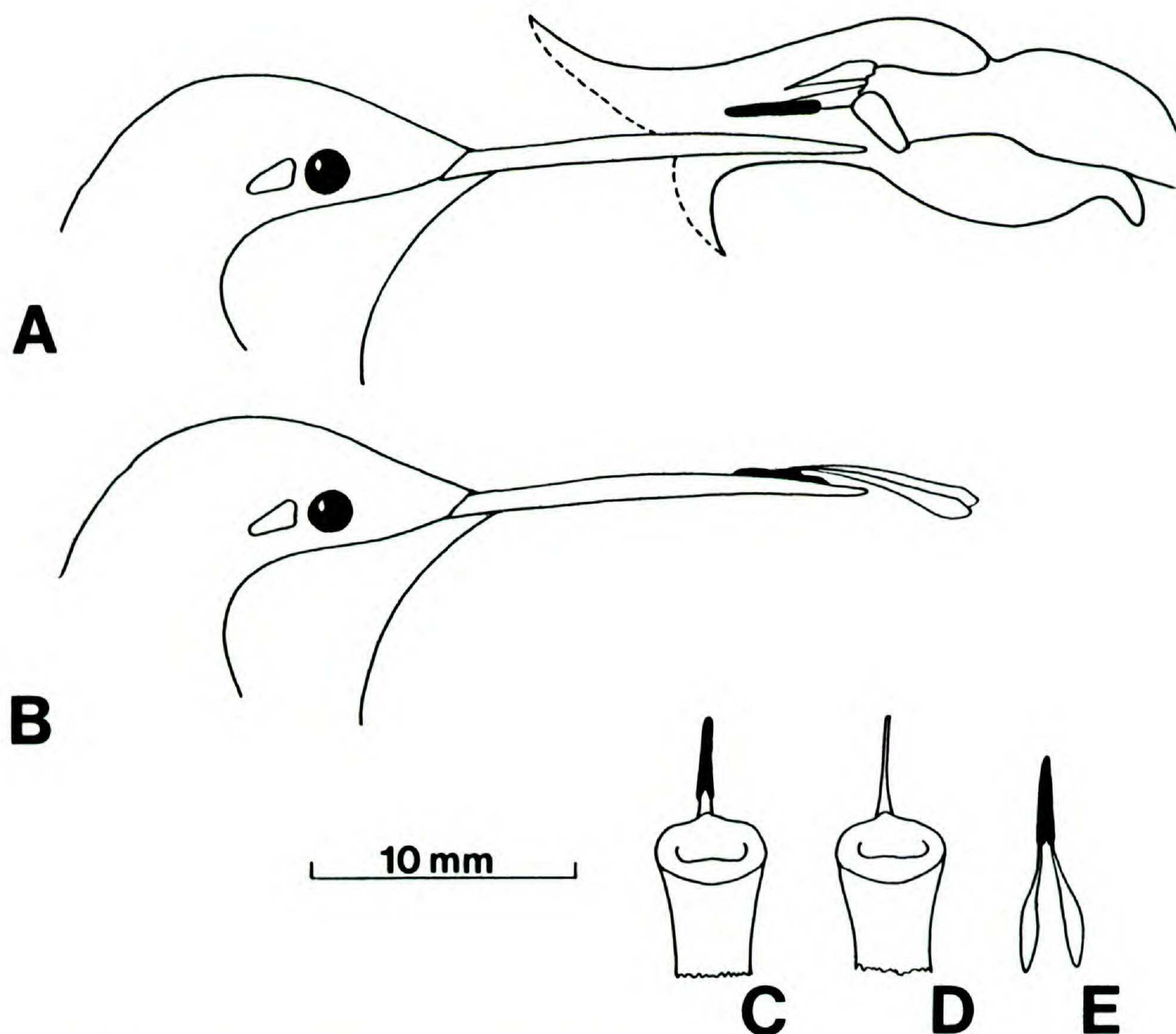


FIGURE 3. A, B. Diagrams of a Ruby-throated Hummingbird (*Archilochus colubris*) removing pollinia from a flower of *Sacoila lanceolata* var. *lanceolata*. —A. Bird with bill inserted in flower, prior to upward movement that will bring it into contact with the viscidium (darkened). —B. Bird with pollinia attached near tip of bill. —C. Column viewed from below prior to removal of pollinarium, the rostellum inserted into the viscidium. —D. Column viewed from below after removal of pollinarium leaving the long narrow rostellum. —E. Pollinarium viewed from below showing viscidium (darkened) and pollinia. All diagrams based on material from Sarasota Co., Florida.

POLLINATION EXPERIMENTS

Pollination was clearly necessary for seed development in *S. lanceolata* var. *lanceolata* from central Guyana (Table 1). In these pollinator-dependent plants, the flowers last for 10–15 days in the absence of pollination. Pollination at any time is followed by fading in two or three days.

In *S. lanceolata* var. *lanceolata* from southern Florida, seed developed regardless of pollinarium removal (Table 1), and these plants were clearly autonomously agamospermic. The flowers lasted 5–15 days in the absence of pollination, but pollination resulted in fading within two days.

Seed development occurred in undisturbed flowers of *S. lanceolata* var. *paludicola*, but not when the pollinarium was removed from the flower at an early stage (Table 1), indicating

autogamy (self-pollination) or pseudogamy (pollination-induced agamospermy) in this variety. Self-pollination occurred after the flowers had been open for one or two days. The flowers are short-lived, lasting for approximately five days. The mechanism of self-pollination is a simple one involving contact between the stigmatic surface and the pollen masses (Figs. 4B, 5). Such contact is not possible in var. *lanceolata* because of the separation resulting from the relative lengths of the pollinia and the basal part of the column (Fig. 4A).

ANATOMICAL STUDY

The Guyana plants of var. *lanceolata* and plants of var. *paludicola* from southern Florida demonstrated a normal sequence of pollination, pol-

TABLE 1. Pollination experiments with *Sacoila lanceolata*.

| Treatment | No. of Plants | No. of Ovaries | No./% Ovaries Expanded* | No./% Ovaries with Seed* | % Sacs with Embryos* |
|--|---------------|----------------|-------------------------|--------------------------|----------------------|
| <i>S. lanceolata</i> var. <i>lanceolata</i> —Guyana | | | | | |
| Undisturbed | 3 | 6 | 0/0 | 0/0 | 0 |
| Pollen removed | 3 | 6 | 0/0 | 0/0 | 0 |
| Self-pollination | 3 | 6 | 6/100 | 4/66 | 50–100 |
| Geitonogamous-pollination | 3 | 6 | 6/100 | 4/66 | 60–100 |
| Cross-pollination | 3 | 6 | 6/100 | 4/66 | 60–100 |
| <i>S. lanceolata</i> var. <i>lanceolata</i> —South Florida | | | | | |
| Undisturbed | 60 | 200 | 200/100 | 200/100 | 90–100 |
| Pollen removed | 60 | 180 | 180/100 | 180/100 | 97–100 |
| Self-pollination | 60 | 180 | 180/100 | 180/100 | 96–100 |
| Geitonogamous-pollination | 60 | 180 | 180/100 | 180/100 | 97–100 |
| Cross-pollination | 60 | 180 | 180/100 | 180/100 | 97–100 |
| <i>S. lanceolata</i> var. <i>paludicola</i> —South Florida | | | | | |
| Undisturbed | 6 | 25 | 25/10 | 25/10 | 95–100 |
| Pollen removed | 6 | 12 | 0/0 | 0/0 | 0 |
| Self-pollination | 6 | 12 | 12/100 | 12/100 | 95–100 |
| Geitonogamous-pollination | 6 | 12 | 12/100 | 12/100 | 95–100 |
| Cross-pollination | 6 | 12 | 12/100 | 12/100 | 95–100 |

* As a percentage of the total ovaries tested.

len tube growth, fertilization, and embryo development (see Catling, 1982). In plants of var. *lanceolata* from Florida, the gametophyte degenerated and one or more cells of the inner integument proliferated to become embryos. The proliferation of these cells was indicated by the more deeply staining protoplasts, relatively large nuclei, and well-developed nucleoli (Fig. 6). Proliferation had initiated in the ovaries of flowers open for five days and may have initiated earlier but was not evident in mature ovaries with buds on the point of opening. Using ovaries of increasing age within an inflorescence, it was possible to trace the darkly staining and proliferating micropylar integument to embryos in mature seeds. The seed resulting from adventitious embryony (Fig. 7C) differs from that resulting from fertilization (Fig. 7A, B) in having a proportion of the seeds polyembryonic (range 28–95%, mean 71.3%, standard deviation 17, based on 15 flowers representing 15 different southern Florida populations).

Five capsules from flowers cross-pollinated on the first day of opening and five capsules from flowers from which the pollinarium was removed demonstrated similar levels of polyembryony (range 56–94%, mean 73.5%, standard deviation 17.9; range 30–84%, mean 57.2%, standard deviation 23.5, respectively).

STUDY OF DRIED MATERIAL

Many more collections and some supporting fieldwork would be necessary to allow a reliable assessment of the distribution of different breeding systems throughout the range of *S. lanceolata*. However, an appraisal of the extent to which the breeding systems of the southern Florida populations are unique was possible with the material examined.

Agamospermy, as evidenced by polyembryonic seed, was found in all fruiting plants from Florida and in some plants from Guatemala, Belize (British Honduras), and Bolivia. In some cases this was associated with non-opening (i.e., cleistapogamous, see Sheviak, 1982) flowers (for example, district of Peten, Guatemala, 12 June 1933, *C. L. Lundell 3896*, MICH). The occurrence of agamospermy within the main tropical range is not clearly associated with relatively high altitude, a situation that involves some of the same effects as high latitude, and the sample is not large enough or sufficiently well documented to reliably reflect a trend.

Relatively small flowers (lateral sepals 14–17 mm long), suggestive of self-pollination, were characteristic of plants from a number of Caribbean islands (for example, Bahamas, St. Vincent, based on specimens at AMES and FTG). Limited

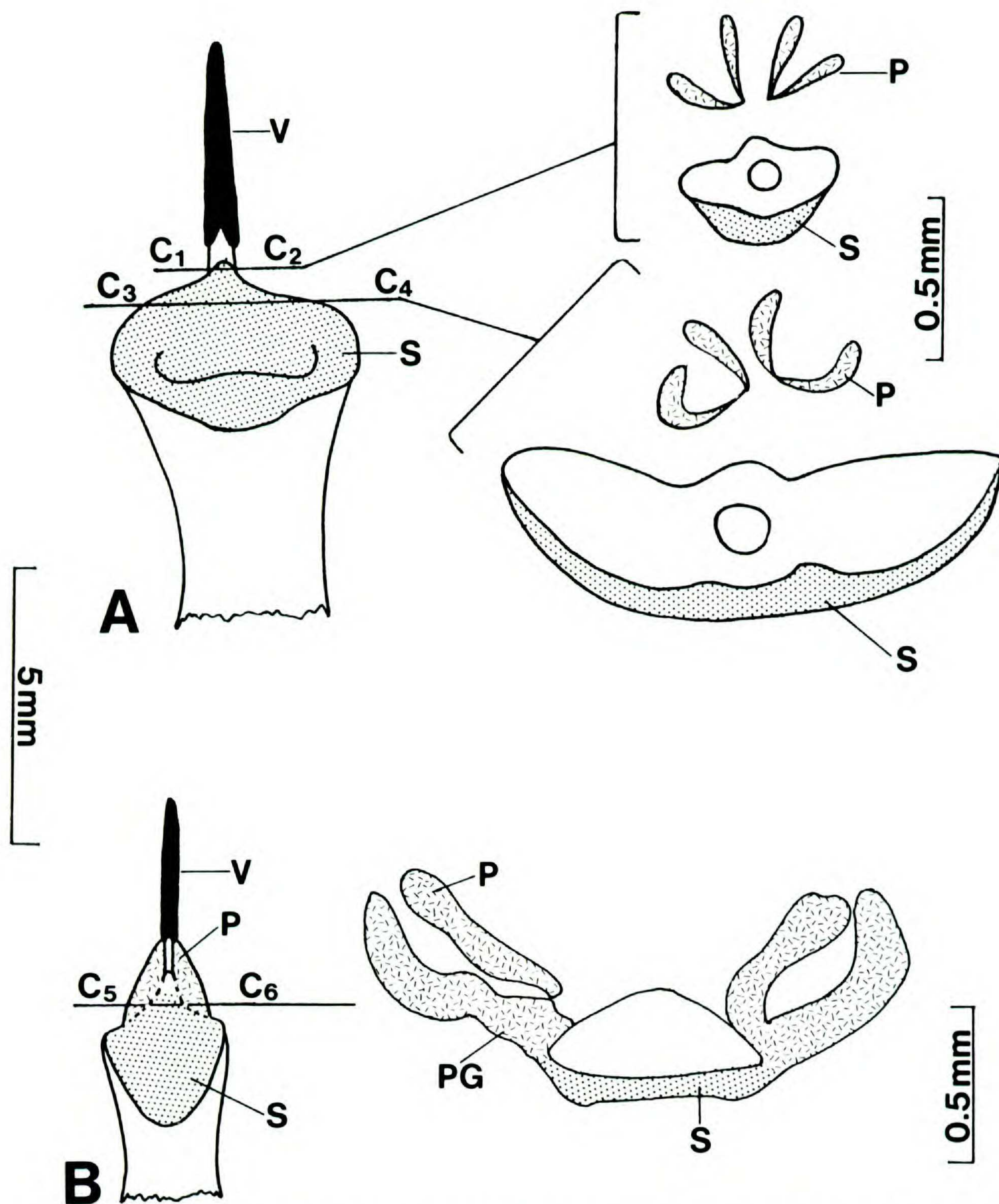


FIGURE 4. A. Column of *Sacoila lanceolata* var. *lanceolata* viewed from below (left) and diagrams of cross-sections (right) based on material from Sarasota Co., Florida. — B. Column of *Sacoila lanceolata* var. *paludicola* viewed from below and diagram of cross-section (right) of flowers originating from Collier Co., Florida. C₁–C₆, cross-sections illustrated on the right-hand side of the figure: P, pollinarium; PG, pollen germinating; S, stigmatic surface; V, viscidium.

fruit set, suggestive of obligate cross-pollination, was restricted to Costa Rica and northern South America.

DISCUSSION

Agamospermy is uncommon in the orchid family, having been previously reported only in *Zeuxine*, *Nigritella*, and *Spiranthes* (Maheshwari, 1952; Catling, 1982), *Prasophyllum* (Bates, 1984a), *Microtus* (Bates, 1984b), *Paracaleana*

(Jones, 1977), *Dactylorhiza* (Dressler, 1981), *Zygopetalum* (Dressler, 1981), and *Pterygodium* (Schelpe, 1970). Autogamy is much more prevalent than agamospermy in vascular plants generally and in the orchid family, where it has been reported in over 60 genera (Catling, unpubl. data).

In *S. lanceolata* var. *lanceolata*, it is not known whether agamospermy is facultative. Although there is no evidence of seed resulting from cross-fertilization in terms of a lower incidence of poly-

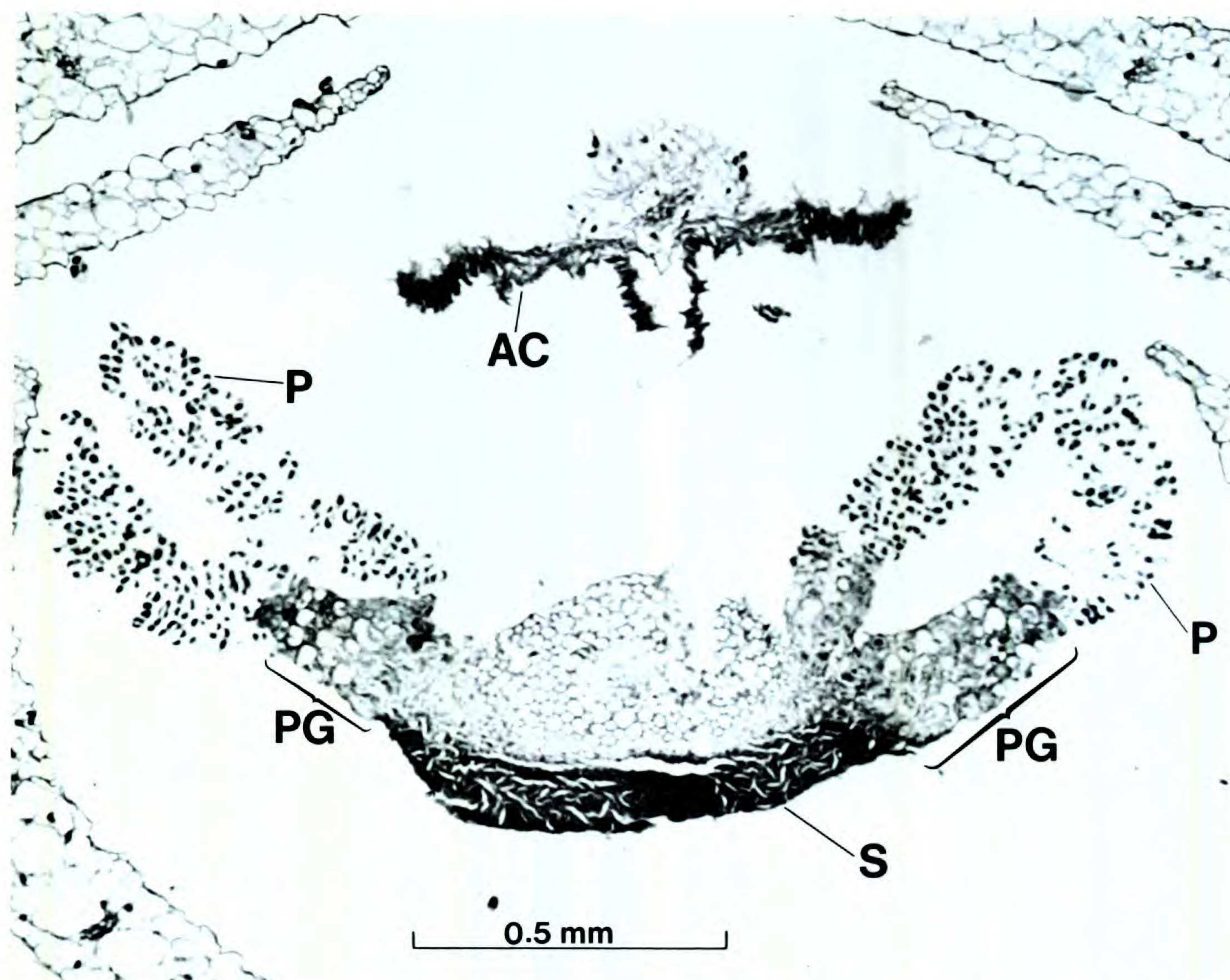


FIGURE 5. Cross-section of column of *S. lanceolata* var. *paludicola*, from Collier Co., Florida. This section represents the position C₅–C₆ in Figure 4B. AC, anther cap; P, pollinarium; PG, pollen germinating; S, stigmatic surface.

embryony, this may have been the result of cross-pollinations using genetically identical individuals with some degree of self-incompatibility. Although the crossings involved plants from different localities in southern Florida, it is conceivable that the different populations had the same agamospermic origin and are genetically identical.

Pollination by hummingbirds in *S. lanceolata* is to be expected on the basis of various floral features such as the tubular, horizontally oriented, reddish flowers without internal marking and lacking odor (Austin, 1975; Pijl & Dodson, 1966), but no previous observations of hummingbird pollination have been reported. The only feature of characteristically bird-pollinated orchid flowers that is lacking is a dark pollinarium (Dressler, 1971), that of *S. lanceolata* being pale yellow. Although the observation of hummingbird-pollination reported here involved transplanted and cultivated plants, there seems to be no reason to

doubt that these observations are indicative of the pollination mechanism in various other situations where one or more species of hummingbirds are available.

The suggestion of a lack of natural pollinators in southern Florida pineland is of interest insofar as it may provide an explanation for the pollinator-independent breeding systems. Although self-pollination and agamospermy are associated with pollinator-paucity and colonization of new territory (for example, Allard, 1965; Jain, 1976; Lloyd, 1978) the actual absence of pollinators has not often been well established (for example, Kevan, 1972); nor has “newness” been quantified.

In the southern Florida pinelands in May, *Erythrina herbacea* and *Ipomea microdactyla* are among the few characteristic hummingbird blossoms available, and these species were not observed near colonies of var. *lanceolata*. Only one species of hummingbird (*A. colubris*) is present,

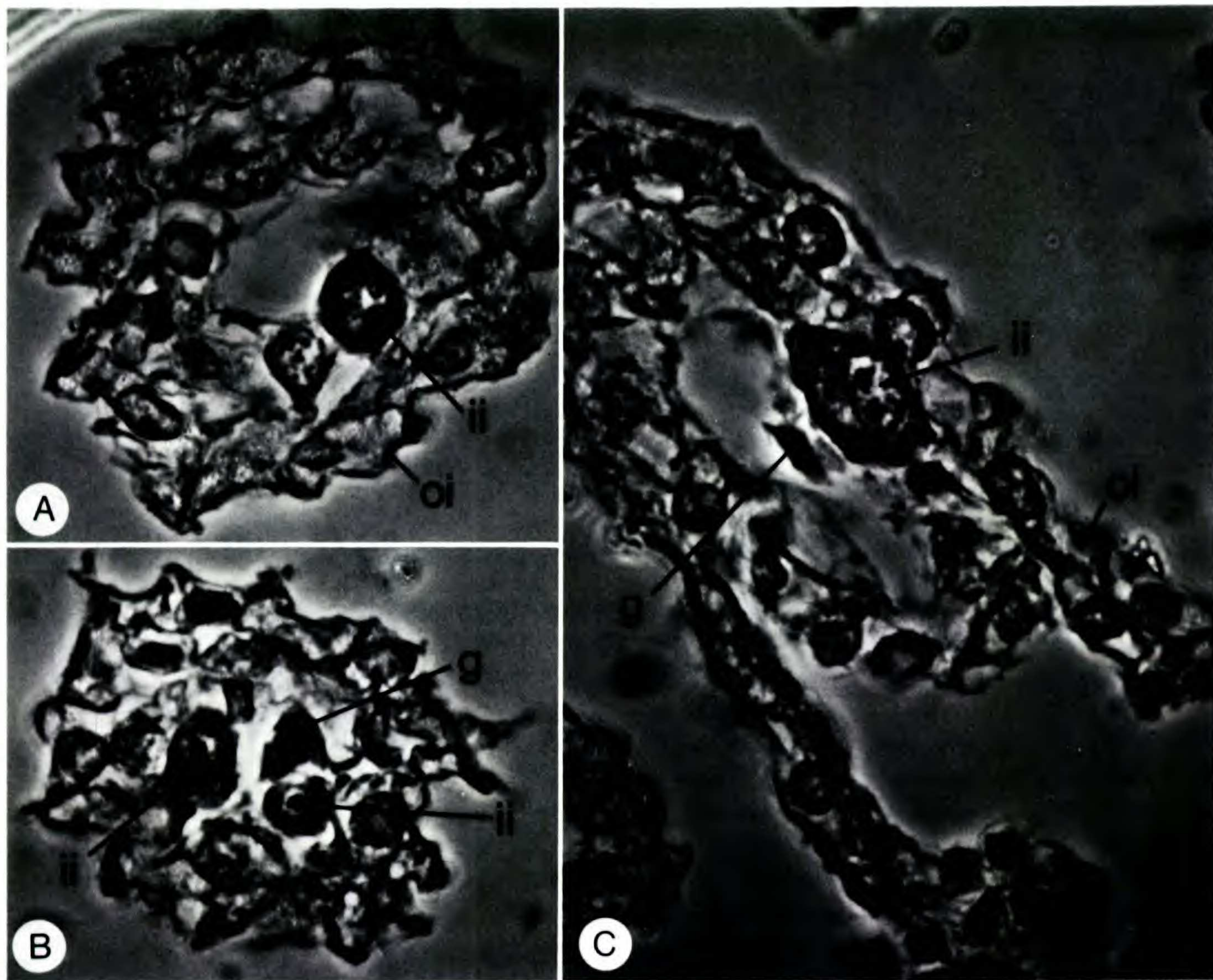


FIGURE 6. A, B. Cross-sections of ovules of *S. lanceolata* var. *lanceolata* from Sarasota Co., Florida.—C. Longitudinal section. g = degenerate gametophyte, ii = proliferating inner integument, oi = outer integument. Material from Sarasota Co., Florida.

and by April and May it has already migrated through the area (Austin, 1975). Breeding of *A. colubris* south of Lake Okeechobee may be very localized (Sprunt, 1954), and there is very little evidence of breeding in southern Florida (Robertson, 1974). Thus there is relatively little to attract hummingbirds to the vicinity of many *S. lanceolata* colonies in southern Florida during the May blooming period, and there is only one potential hummingbird pollinator, which is apparently not abundant. The var. *paludicola* also exists in the absence of a diverse hummingbird-pollinated flora in southern Florida, although a few bromeliads exhibiting the syndrome do flower simultaneously in the hammocks. The situation over much of the range of var. *lanceolata* is quite different since many different hummingbird species are available and there is a diversity and continuity of hummingbird-pollinated blos-

soms on a year-round basis (Grant & Grant, 1968).

Populations of five other tropical orchids (*Epidendrum rigidum*, *E. nocturnum*, *Encyclia cochleata* var. *triandra*, *E. boothiana* var. *erythronoides* and *Bletia purpurea*) in many parts of southern Florida possess a column structure that promotes self-pollination. This is in contrast to parts of (or all of) the warmer continental neotropics where these same species have a column structure adapted to cross-pollination, or where this latter column structure is at least predominant (Luer, 1971b, 1972; Pijl & Dodson, 1966; pers. obs.). Pollinators are not clearly lacking in the case of these species. It is possible that continual near extinctions due to frost (Singleton, 1936; Stowers & Le Vasseur, 1983), hurricanes (Craighead & Gilbert, 1962; Alexander, 1967) and sea-level fluctuations (Fairbridge, 1974;

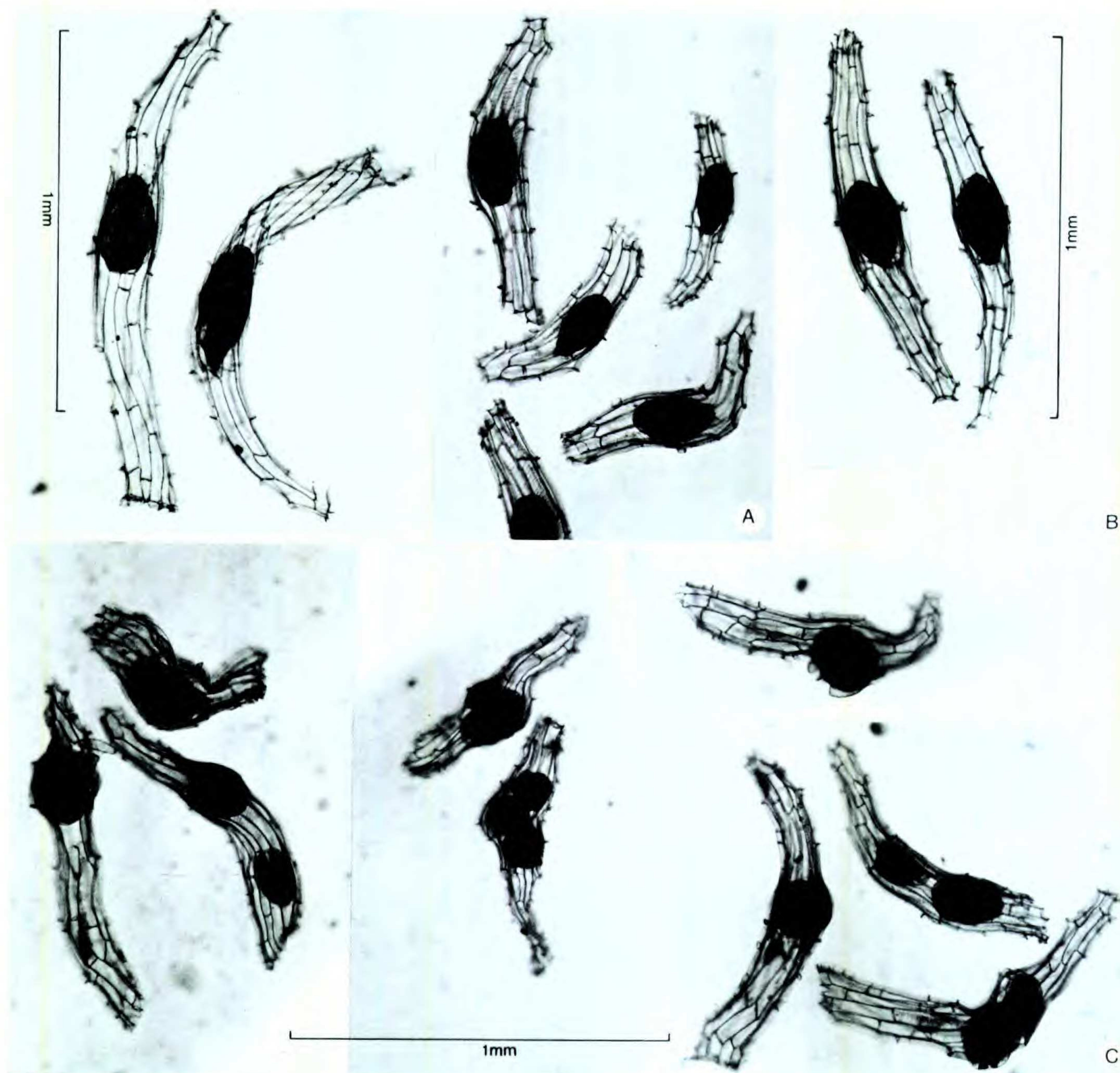


FIGURE 7. A, B. Seed of *Sacoila lanceolata* var. *paludicola*. — A. Collier Co., Florida. — B. Dade Co., Florida. — C. Seed of *S. lanceolata* var. *lanceolata* from Sarasota Co., Florida.

Long, 1974) resulted in a strong selection for colonizing ability, regardless of pollinator-availability. With their terrestrial habit and drier elevated habitats, it seems unlikely that the two varieties of *S. lanceolata* would be as strongly influenced by these factors. Consequently pollinator-paucity is considered to provide an adequate explanation for their pollinator-independent breeding systems in southern Florida.

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